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ORIGINAL ARTICLE

Windborne migration of Auchenorrhyncha (Hemiptera) over Britain

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Abstract. Planthoppers (Delphacidae), leafhoppers (Cicadellidae) and froghoppers (Aphrophoridae) (Hemiptera: Auchenorrhyncha) caught during day and night sampling at a height of 200 m above ground at Cardington, Bedfordshire, UK, during eight summers (between 1999 and 2007) were consolidated with high-altitude catches made over England in the 1930s. Comparisons were made with other auchenorrhynchan trapping results from northwest Europe, which were indicative of migration. The migratory abilities in the species concerned were then interpreted in terms of various life-history traits or ecological characteristics, such as ontogenetic, diel and seasonal flight patterns, voltinism, habitat preferences, and host plant affinity. In contrast to some other areas of the world (North America, East Asia), the migratory abilities of most Auchenorrhyncha species in northwest Europe is poorly understood, and thus the present study draws together, and complements, fragmentary information on this topic as a basis for further research.

INTRODUCTION

Some members of the Auchenorrhyncha (Hemiptera) are noted long-distance migrants – they can ascend to high altitudes (Glick, 1939, 1960; Riley et al., 1991; Reynolds et al., 1999; Drake & Reynolds, 2012), and are able to maintain continuous wing-beating for long periods of time while the wind transports them over great distances. In fact, the migration of the delphacid rice pests *Sogatella furcifera* (Horváth) (white-backed planthopper), *Nilaparvata lugens* (Stål) (brown planthopper) and *Laodelphax striatella* (Fallén) (small brown planthopper) from the East Asian mainland to Japan each year (Kisimoto & Rosenberg, 1994; Otuka et al., 2010; Otuka, 2013), covering an overwater movement of ~1000 km, is one of the longest non-stop journeys in relation to body size of any animal migrant. Another remarkable instance was the mass invasion of the mid-Atlantic Ascension Island by the cicadellid *Balclutha pauxilla* Lindberg, probably from southwest Africa, more than 3000 km away (Ghauri, 1983). In North America, the annual long-distance migrations of the cicadellids *Empoasca fabae* (Harris) (potato leafhopper), *Macrosteles quadrilineatus* Forbes (= *M. fascifrons*; six-spotted or aster leafhopper) and *Circulifer tenellus* (Baker) (beet leafhopper) are well-known (Glick, 1960; Johnson, 1969; Taylor, 1985, 1989; Carlson et al., 1992; Taylor et al., 1995; Shields & Testa, 1999).

Some of these plant- and leafhopper species make long-range poleward movements each summer from continuous breeding zones at lower latitudes, and they can be of immense economic importance due to their role as vectors of plant viruses, bacteria, and other pathogens or, in some cases, due to direct feeding damage to crops (e.g. Heong & Hardy, 2009; Otuka, 2013; Chasen et al., 2014). In Africa, *Cicadulina* leafhoppers are major vectors of maize streak disease; Rose (1978) investigated the flight durations of various species and morphs and found that some of the long-flying forms could fly continuously for several hours, although the frequency distribution of durations was markedly skewed towards short-duration flights.

In Europe, damage to crops due to migrant Auchenorrhyncha is less significant than in the above-mentioned regions (but see Brčák, 1979; Lindsten, 1979) and, consequently, migration has been less intensively studied. Moreover, most of the detailed studies that have been made (Raatikainen, 1967; Raatikainen & Vasarainen, 1973; Waloff, 1973; della Giustina & Balasse, 1999), have involved trapping at relatively low heights above ground (≤12.3 m); sampling Auchenorrhyncha above the atmos-

pheric surface layer is seldom undertaken. An exception was the study by Günthart (1988) who analysed the vertical distribution of leafhoppers, trapped up to 155 m above ground on a meteorological mast near Basle in Switzerland, but here the fauna was very different to that found in the studies in Britain, with only *Conosanus obsoletus* (Kirschbaum) (one specimen caught by Freeman, 1939) in common. We also note the capture of the leafhopper *Arthaldeus pascuellus* (Fallén) (referred to as *Deltocephalus pascuellus*) at 1000–1200 m over northern France in June 1934 during trapping from an aeroplane (Berland, 1935).

Even among macropterous flight-capable Auchenorrhyncha, the majority of flights undertaken are short duration 'flits' (sensu Southwood, 1960; Waloff, 1973) which are 'appetitive' in nature (i.e. low-altitude local flights concerned with feeding and reproduction) or, perhaps, some very short-range dispersal events. The present paper is concerned with windborne migratory movements, and we adopt the individual-based behavioural definition of migration formulated by J.S. Kennedy and developed by H. Dingle (see Dingle, 2014 pp. 14–15). For it to be likely that Auchenorrhyncha individuals are engaged in windborne migration, aerial samples must be taken well above an insect's 'flight boundary layer' (Taylor, 1974) – the layer of the atmosphere near the ground surface or plant canopy where the ambient wind speed is lower than the insect's self-powered flight speed. Drawing upon the work of L.R. Taylor and others, Teraguschi (1986) in his study of leafhoppers of an old-field site in Ohio, USA, espouses the view "that the crossing of the flight boundary layer interface is a highly programmed event" so that "aerial abundances are not simple functions of terrestrial abundances" – a standpoint with which we agree (see e.g. Reynolds et al., 2014). Günthart's (1988) samples were taken at several heights simultaneously and extended high above the ground, so she was able to estimate the thickness of the leafhopper flight boundary layer (viz. ~20–30 m). Southwood (1962) considered that Heteroptera caught above ~15 m would be migrants rather than individuals engaged in short-duration 'flitting'. In the aerial sampling studies considered here, the Auchenorrhyncha trapped were flying at least several tens of metres above ground and were thus well above their flight boundary layer.

Some early researchers, sampling at relatively low heights above ground, may not have fully realized the movement potential of these Auchenorrhyncha, resulting in underestimates of migration distances. Insect ascent to the altitudes sampled by us at an updraft-assisted vertical speed of, say, 1 m/s, even if followed by immediate descent, would take a minimum of several minutes, which at ambient wind speeds recorded when hoppers were flying (~7 m/s) would result in a movement of at least several kilometres. Any tendency to maintain flapping flight at altitude would, of course, rapidly extend the migratory ambit.

In the present study, planthoppers (Delphacidae), leafhoppers (Cicadellidae) and froghoppers (Aphrophoridae) were sampled at a height of ca. 200 m above ground over southern England. We integrate these results with those from early (1930s) UK studies in which numbers of Auchenorrhyncha were captured aloft (> 50 m) and which were identified to species level (Hardy & Milne 1938; Freeman, 1939, 1945). We also bring together other scattered records from the literature, which are indicative of migratory activity, for the British species of Auchenorrhyncha. Based on results from previous studies of migration in Auchenorrhyncha, especially in Europe, North America and East Asia, we test the following specific hypotheses:

- volant individuals will either belong to species that are always fully winged or be macropterous individuals of wing-polymorphic species;
- most flight activity will be nocturnal;
- aerial densities of Auchenorrhyncha will be greater under conditions of higher wind speeds, but will be unrelated to wind direction;
- the assemblage of volant Auchenorrhyncha will be characterised by species that are bivoltine, polyphagous and primarily associated with ephemeral or disturbed habitats, and that overwinter as eggs or nymphs rather than adults;
- sex ratios in aerial catches will not depart significantly from 1 : 1.

METHODS

We took aerial samples of insects at ca. 200 m above ground with a drogue net of 1 m diameter aperture suspended from a tethered helium-filled kite-balloon (kytoon) (Fig. 1). The sampling site, at Cardington Airfield (52°06′N, 0°25′W), Shortstown, Bedfordshire, in southern England, has an official aircraft exclusion zone which allowed the kytoon to be flown above the Civil Aviation Authority limit of 60 m. Sampling was carried out in the years 1999, 2000, and 2002–2007, in various months between May and early September, but mostly in July (Table 1). [The aerial netting was designed to support our radar observations (e.g. Hu et al., 2016), and insect numbers detected by the radar were extremely low outside the May–September period.]

Fig. 1. Sampling insects at ca. 200 m above ground by means of a net attached to the tethering line of a 6-m long kytoon. The detachable bag at the end of the net has just been closed-off, prior to winching down of the kytoon to ground level and recovery of the sample. The wind-run meter can be seen suspended below the kytoon tail.

Table 1. Auchenorrhyncha caught at high altitude (ca. 200 m a.g.l) at Cardington, Bedfordshire, UK, 1999–2007.

	Year	1999	2000	2002	2003	2004	2005	2006	2007	Total	Sex	
	Sampling month(s)	July	July	July	August –Sept.	July	June –July	August –Sept.	May– July			
	Total wind-run (km)	2847.2	2524.0	2273.0	2922.1	2610.0	3262.0	1370.0	2188.0		F	M
Family	Species											
Delphacidae	*Javesella pellucida* (Fab.)	17	3	15	1	2	7		77	122	63	59
	Javesella dubia (Kirschbaum)						1			1		1
	Muellerianella brevipennis (Boheman)								2	2	1	1
Cicadellidae	*Anaceratagallia ribauti* (Ossiannilsson)							1		1	1	
	Anoscopus albifrons (L.)			1		1	2			4	4	
	Deltocephalus pulicaris (Fallén)	2			1			1		4	1	3
	Arthaldeus pascuellus (Fallén)				9		13	1		23	19	4
	Psammotettix confinis (Dahlbom)		1		1		1			3	1	2
	Psammotettix nodosus (Ribaut)	1								1	1	
	Euscelis incisus (Kirshbaum)				1	1				2	2	
	Streptanus sordidus (Zetterstedt)						1			1		1
	Athysanus argentarius Metcalf	1								1		1
	Macrosteles sp.						2			2	2	
	Empoasca decipiens (Paoli)			1		1				2	2	
	Eurhadina pulchella (Fallén)			1						1	1	
	Eupteryx atropunctata (Goeze)						2		1	3		3
	Eupteryx urticae (F.)						3			3	2	1
	Eupterycyba jucunda (Herrich-Schaeffer)					1				1	1	
	Lindbergina aurovittata (Douglas)					2				2		2
	Fagocyba cruenta (Herrich-Schaeffer)			1						1	1	
	Edwardsiana sp.						1		1	2	2	
	Alnetoidea alneti (Dahlbom)			1		1				2	2	
	Zyginidia scutellaris (Herrich-Schaeffer)			2			4		1	7	4	3
Aphrophoridae	*Neophilaenus lineatus* (L.)			1						1		1
Total		21	4	23	13	9	37	3	82	192	110	82
Mean density (numbers per 10^5 m^3)		3.7	3.1	4.3	3.5	4.7	4.3	2.6	13.5			

For aerial sampling purposes, the 24-h period was generally divided up as follows: 1 h around dusk (~21.00–22.00 h BST in July); night-time after the dusk period (various durations, occasionally until dawn); 'morning' (10.00–14:00 h), and afternoon (14:00–18:00). At the end of each sample period, the rear end of the net was closed off with a radio-controlled strangling device, and the kytoon was winched down to near ground level. A detachable bag containing the insect catch was unzipped from the end of the net and placed in a plastic killing bottle, and the wind run (in kilometres) was read off a meter (which was also suspended from the kytoon). The wind-run measurement for each sample period allowed the airflow through the net to be estimated so that catch numbers could be converted to aerial densities. Further details of kytoon-flying and aerial sampling procedures can be found elsewhere (Chapman et al., 2004; Reynolds et al., 2013). For our analyses, wind speeds were categorized as 'Low' (0 – < 3 m/s), 'Medium' (3 – < 5 m/s), 'Medium-high' (5 – < 8 m/s), and 'High' (≥ 8 m/s). Wind directions were categorised as North (315–45°), East (45–135°), South (135–225°), and West (225–315°).

A night-time sampling height of 200 m was chosen in order to take advantage of any layers of insects developing in the warm, fast-moving air (the boundary layer wind maximum) which tends to form near the top of the surface temperature inversion in clear weather (Drake & Reynolds, 2012) – it was sensible to position the net within this airstream, rather than in the colder and stiller air nearer the ground. The choice of sampling height during the day is more arbitrary (because migrating insects may be circulated through various altitudes by convection), but the standard height of about 200 m was convenient and it was high enough to avoid captures of insects engaged in appetitive flights near the ground. The actual periods selected for sampling depended on the weather: apart from cold or wet conditions, when insect migration does not occur to any appreciable extent in Britain, kytoon-flying was not possible at times of significant lightning risk and during very strong winds. On a few days, winds at altitude proved to be too light (i.e. below ~3 m/s) for efficient netting.

In the early UK studies, Hardy & Milne (1938) used nets attached to kites, and samples containing Auchenorrhyncha were taken at various heights between 76 and 610 m at sites near Hull (Yorkshire), Dover (Kent) and Tetney (Lincolnshire). Freeman (1939, 1945) attached nets to tall radio masts at Tetney at three heights (i.e. 3, 54 and 84 m), but only samples taken at his two upper heights were considered here because individuals caught at 3 m may have been engaged in appetitive flight rather than migration.

Catches from Cardington were sorted and preserved in a mixture of 95% ethanol and 5% glycerol. Auchenorrhyncha present in the samples were later identified – by M.A. Salmon for 1999 samples, otherwise by A.J.A.S – using Le Quesne (1960, 1965, 1969) and Le Quesne & Payne (1981). All specimens were identified to species with the exception of female *Macrosteles* and *Edwardsiana* which cannot be reliably determined beyond genus level. The nomenclature follows Wilson et al. (2015).

Auchenorrhyncha aerial densities obtained from the Cardington samples were compared for time of day categories, wind speed categories, and wind directions, using analyses of deviance based on generalised linear models with quasipoisson errors (R Core Team, 2016). Tukey multiple comparisons derived from these generalised linear models used the R multcomp package (Hothorn et al., 2008). Departure of sex-ratios from 1 : 1 in our samples was tested using chi square goodness-of-fit tests; it was not possible to include data from the earlier studies because they did not enumerate the sexes separately. Calculations of Shannon diversity and evenness indexes and Sørensen's index of similarity follow Magurran (2003).

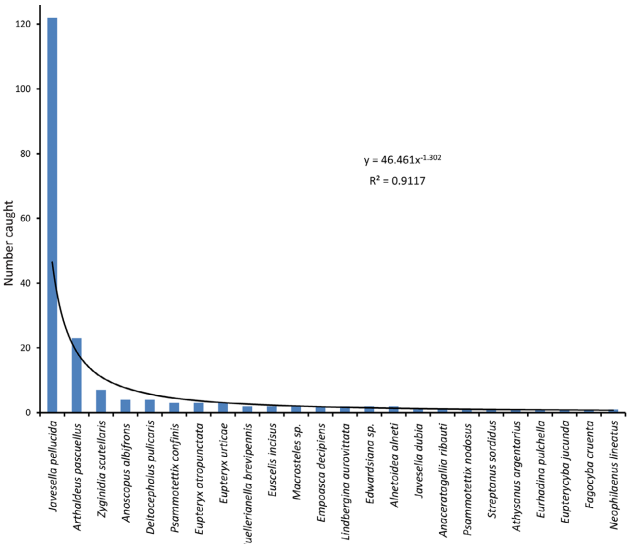

Fig. 2. The rank-abundance curve for Auchenorrhyncha species in aerial samples taken at Cardington, Bedfordshire, 1999–2007. A power-law trendline has been fitted to the data.

RESULTS

A total of 192 individual Auchenorrhyncha across 24 species were caught during the eight years of the present study at Cardington (Table 1). In comparison, 35 specimens of 16 species of Heteroptera were caught in the same samples (Reynolds et al., 2013). All Auchenorrhyncha specimens were macropterous including those of strongly wing-polymorphic species such as *Javesella pellucida*.

Aerial densities

The aerial density of Auchenorrhyncha in our samples between 1999 and 2007 ranged between 3.1 and 4.7 per 10^5 m^3 (Table 1). The average density for the 2007 season showed a higher value (13.5 per 10^5 m^3) due to the presence of large numbers of *J. pellucida.* The highest density for this species was 30 per 10^5 m^3 in a sample taken on the morning of 24 July 2007.

Diel flight periodicity

Diel sampling period had a highly significant effect on the total aerial catch (Table 2) such that 86% of aerial samples that contained hoppers were taken in the morning or afternoon and 10% were taken at dusk (Fig. 3a); the latter may have signified an extension of daytime flight into the dusk period rather than a take-off at dusk. Sampling period also had a highly significant effect on the most common species, *J. pellucida* and *Arthaldeus pascuellus*, both of which were caught exclusively during the day. Only 4% of the samples that contained hoppers were night samples (i.e. taken after 22.00 h BST); the species were singletons

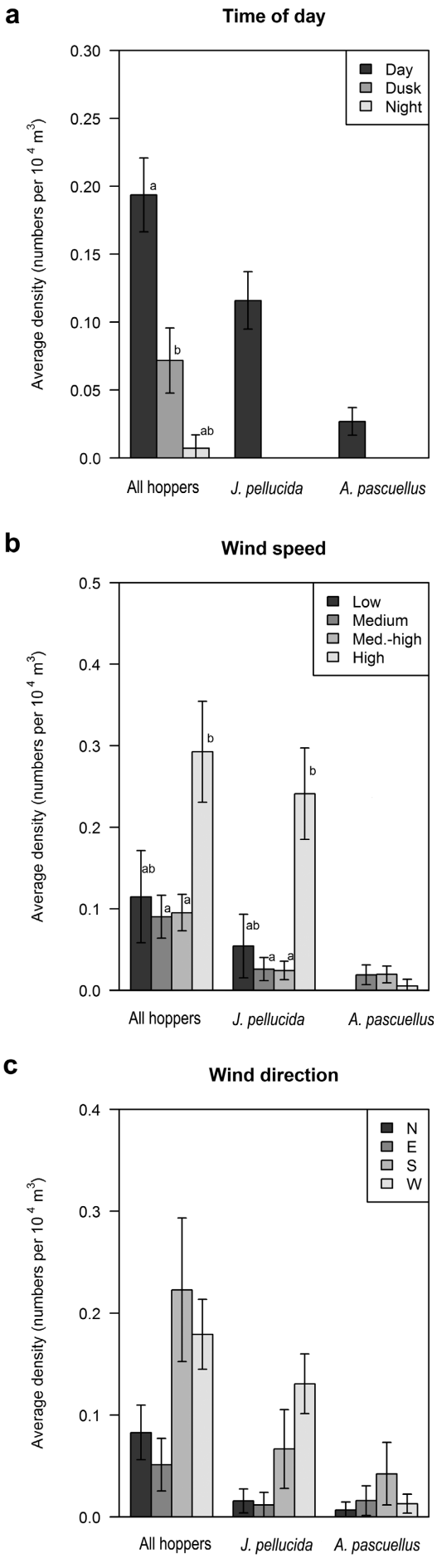

Fig. 3. Aerial densities of all Auchenorrhyncha, and of the commonest two species (*Javesella pellucida* and *Arthaldeus pascuellus*) caught at 200 m a.g.l. at Cardington, Bedfordshire, in relation to (a) time of day/night, (b) wind speed, and (c) wind direction (see 'Methods' for categorization of sampling periods and wind speeds/directions). Error bars indicate standard errors of the mean. Category means sharing lower case letters are not significantly different within species (Tukey's HSD post-hoc test, $p < 0.05$).

Table 2. Tests of the effect of time of day, wind speed and wind direction on aerial densities of Auchenorrhyncha at Cardington for: all species, *Javesella pellucida* and *Arthaldeus pascuellus*.

Test	Factors (levels †)	Post-hoc comparisons	All species	*Javesella pellucida*	*Arthaldeus pascuellus*
ANOVA (p-value associated with F-statistic)	Sampling period (daytime, dusk, or night)	—	$F(2, 274) = 9.64$, $p < 0.001$	$F(2, 274) = 12.84$, $p < 0.001$	$F(2, 274) = 13.22$, $p < 0.001$
Multiple comparison of means: Tukey HSD contrasts	—	Daytime / dusk	$z = –2.35$, corrected p = 0.042	all NS	all NS
		Daytime / night	NS		
		Dusk / night	NS		
ANOVA (p-value associated with F-statistic)	Wind speeds (low, medium, medium-high, or high)	—	$F(3, 273) = 4.17$, $p = 0.007$	$F(3, 273) = 8.04$, $p < 0.001$	NS
Multiple comparison of means: Tukey HSD contrasts	—	Medium / high	$z = –2.95$, corrected p = 0.015	z = –3.27, corrected p = 0.006	all NS
		Medium-high / high	$z = –3.22$, corrected p = 0.006	z = –3.85, corrected p < 0.001	
		All other wind speed comparisons	NS	NS	
ANOVA (p-value associated with F-statistic)	Wind direction (N, E, S, W)	—	$F(3, 273) = 3.18$, $p = 0.024$	$F(3, 273) = 4.97$, $p = 0.002$	NS
Multiple comparison of means: Tukey HSD contrasts	—	All wind direction comparisons	NS	NS	

† For definitions of levels, see Methods section.

of *Psammotettix confinis, P. nodosus* and *Empoasca decipiens*.

Effects of wind speed and direction

The aerial densities of Auchenorrhyncha over Cardington were significantly higher on occasions with high wind speeds, both for all species combined and for *J. pellucida* alone (but not for *A. pascuellus*) (Fig. 3b, Table 2); for example, there were significant Tukey HSD contrasts between hopper densities aloft in wind speeds of 5–8 m/s and speeds ≥ 8 m/s. Wind direction had a significant effect on numbers of all species combined and on *J. pellucida* in particular, but no significant contrasts emerged in the Tukey comparisons between particular wind directions (Fig. 3c, Table 2).

Species composition of aerial samples

Of the 24 species of Auchenorrhyncha caught at Cardington, the majority were leafhoppers (Cicadellidae, n = 20) compared to planthoppers (Delphacidae, n = 3) and froghoppers (Aphrophoridae, n = 1). A rather typically shaped rank-abundance curve was obtained from these data (Fig. 2): only two species were at all frequent, with a long tail of species represented in low numbers or as singletons. The delphacid *J. pellucida* was by far the most frequently caught species (122 individuals) with the cicadellids *A. pascuellus* and *Zyginidia scutellaris* contributing the second and third highest numbers of specimens (23 and 7, respectively). Shannon diversity (H') and evenness (E) were 0.69 and 0.50 respectively.

Table 3 compares our aerial catches with those made over England in the 1930s by Hardy & Milne (1938) and Freeman (1939, 1945). The commonest ten species, in order of the grand total caught across the earlier studies and ours were: *J. pellucida*, *A. pascuellus, Deltocephalus pulicaris, Psammotettix alienus*, *Eupteryx atropunctata*, *Neophilaenus lineatus*, *Euscelis incisus*, *Z. scutellaris*, *P. confinis* and *Cicadula quadrinotata*. Sørensen's qualitative index of community similarity between our samples and those of Freeman (1939, 1945) was low (0.38); only eight out of 34 species across the two communities were recorded at both sites. The sample size recorded by Hardy & Milne (1938) was too small (n = 19) to justify comparison with the other studies.

We also compared our data to the catches of Auchenorrhyncha in Rothamsted-type suction traps at 12.2 m above ground in France based on one complete year of sampling at about twelve sites (della Giustina & Balasse, 1999). The standardized height of this suction trap was originally chosen in order to sample small insects (particularly aphids) that were likely to be long-distance migrants, i.e. the trap was designed so that the entrance was above the height of most local insect flight (Macauley et al., 1988). In spite of the two orders of magnitude difference between the sample size in England (n = 192) and that in France (n = 10,790), the latter were dominated by a similar list of species (totals in brackets): *Z. scutellaris* (4577), *J. pellucida* (3268) and *Empoasca* spp. (890) (including some *Empoasca decipiens*). Other species caught in England were also caught reasonably frequently in the French suction traps: *Javesella dubia* (184), *Lindbergina aurovittata* (97), *Psammotettix alienus* (30) and *P. confinis* (23).

Phenology, voltinism, sex-ratio and overwintering stage

Nearly all the species caught in aerial netting over England are known to undergo two or more annual generations routinely or facultatively (Table 4). Most specimens of *J. pellucida* were caught in mid to late July, particularly in late July 2007. The sexes migrated in approximately equal proportions (63♀ : 59♂; $\chi^2_{(1)} = 0.13$, p = 0.72). In contrast, we caught *A. pascuellus* from mid-June to early July, and

Table 3. Comparison of catches of Auchenorrhyncha obtained during some aerial trapping studies over England.

Study reference		Freeman, 1939, 1945		Hardy & Milne, 1938		Present study		Totals
Sampling location		Tetney, near Grimsby		Hull, Tetney, Dover		Cardington, Bedfordshire		
Year(s)		1934, 1935		1932–1935		1999, 2000, 2002–2007		
Sampling period		May–September		June–October		May–early September		
Time of sampling		Day only		Day only		Day and night		
Height of sampling		54 and 84 m only*		61– 610 m		ca. 200 m		
Auchenorrhynchan superfamily, family & species	Species name in Freeman, or Hardy & Milne (if different)	Number	%	Number	%	Number	%	
Fulgoroidea								
Delphacidae								
Kelisia vittipennis (Sahlberg)				1	5.26			1
Muellerianella brevipennis (Boheman)						2	1.04	2
Javesella pellucida (F.)	*Liburnia pellucida*	3	1.97	3	15.79	122	63.54	128
Javesella dubia (Kirschbaum)						1	0.52	1
Genus uncertain†	*Liburnia* sp.	1	0.66					
Membracoidea								
Cicadellidae								
Anaceratagallia ribauti (Ossiannilsson)						1	0.52	1
Anoscopus albifrons (L.)						4	2.08	4
Deltocephalus pulicaris (Fallén)		20	13.16	2	10.53	4	2.08	26
Turrutus socialis (Flor)	*Deltocephalus socialis*			1	5.26			1
Errastunus ocellaris (Fallén)	*Deltocephalus ocellaris*	5	3.29					5
Arthaldeus pascuellus (Fallén)	*Deltocephalus pascuellus*	11	7.24	1	5.26	23	11.98	35
Psammotettix confinis (Dahlbom)	*Deltocephalus thenii*	5	3.29			3	1.56	8
Psammotettix nodosus (Ribaut)						1	0.52	1
Psammotettix alienus (Dahlbom)	*Deltocephalus striatus*	19	12.50	1	5.26			20
Conosanus obsoletus (Kirshbaum)	*Athysanus obsoletus*	1	0.66					1
Euscelis incisus (Kirshbaum)	*Athysanus plebejus*	7	4.61	1	5.26	2	1.04	10
Euscelis lineolatus Brullé	*Athysanus lineolatus*	6	3.95					6
Streptanus aemulans (Kirshbaum)	*Athysanus sahlbergi*	1	0.66					1
Streptanus sordidus (Zetterstedt)						1	0.52	1
Athysanus argentarius Metcalf						1	0.52	1
Rhopalopyx adumbrata (Sahlberg)	*Stictocoris preyssleri*			1	5.26			1
Mocydia crocea (Herrich-Schaeffer)				1	5.26			1
Cicadula quadrinotata (Fab.)	*Limotettix quadrinotata*	1	0.66	1	5.26			2
Elymana sulphurella (Zetterstedt)	*Limotettix sulphurella*	1	0.66					1
Macrosteles sexnotatus (Fallén)	*Cicadula sexnotata*	25	16.45	6	31.58			31
Macrosteles sp.						2	1.04	2
Empoasca decipiens (Paoli)						2	1.04	2
Eurhadina pulchella (Fallén)						1	0.52	1
Eupteryx atropunctata (Goeze)	*Eupteryx atropunctatus*	17	11.18			3	1.56	20
Eupteryx urticae (Fab.)						3	1.56	3
Eupterycyba jucunda (Herrich-Schaeffer)						1	0.52	1
Lindbergina aurovittata (Douglas)						2	1.04	2
Fagocyba cruenta (Herrich-Schaeffer)						1	0.52	1
Edwardsiana sp.						2	1.04	2
Alnetoidea alneti (Dahlbom)						2	1.04	2
Zyginidia scutellaris (Herrich-Schaeffer)	*Erythroneura scutellellaris*	3	1.97			7	3.65	10
Genus uncertain †	*Deltocephalus* spp.	4	2.63					4
Genus uncertain †	*Cicadula* sp.	1	0.66					1
Unidentified cicadellids		6	3.95					6
Cercopoidea								
Aphrophoridae								
Philaenus spumarius (L.)		1	0.66					1
Neophilaenus lineatus (L.)	*Philaenus lineatus*	14	9.21			1	0.52	15
Total Auchenorrhyncha		152	100	19	100	192	100	362
Total insects and % Auchenorrhyncha		7748	1.96	839	2.26	17752	1.08	

* Freeman's samples taken at his lowest height (3 m above ground) were omitted. † The genus given in Freeman (1939) has now been split into several genera.

from late August to early September, but as significantly more females than males (19 : 4, $\chi^2_{(1)} = 9.78$, P = 0.002). The ratio of females to males amongst the remaining species combined was 1.5 : 1 but this difference was not formally significant ($\chi^2_{(1)} = 1.72$, p = 0.19).

The proportion of all species caught in aerial netting over England (Table 4) adopting the different stages (egg, nymph, adult) for overwintering did not differ significantly from the proportions (64%, 19% & 16% respectively) given by Nickel (2003) for the complete Auchenorrhyncha fauna in Germany ($\chi^2_{(2)} = 1.75$, p = 0.42; for this comparison, *Euscelis incisus* was treated as split equally between overwintering in the egg and nymphal stages).

Table 4. Information on habitat, host plant specificity, overwintering stage and number of generations for Auchenorrhyncha species caught by aerial netting over England. Species caught as singletons are not included.

Species (in order of abundance in aerial samples)	Total number caught	Habitat type (in UK) *	Host plant specificity ‡	Over-wintering stage	No. of annual generations	Reference for overwintering stage and voltinism (in England, if available, otherwise Germany)
Javesella pellucida	128	Grassland, sedges, cereal crops	p	N	2	Waloff & Solomon, 1973; Morris, 1990a, b
Arthaldeus pascuellus	35	Grassland	o1	e	2	Waloff & Solomon, 1973
Macrosteles sexnotatus	31	Grassland, clover (*Trifolium* spp.)	p	e	2	Waloff & Solomon, 1973
Deltocephalus pulicaris	26	Grassland, particularly in short grasses	o1	e	2	Waloff, 1973
Psammotettix alienus	20	Grassland	o1	e	2 †	Nickel & Remane, 2002; † 3 generations in a warm year in Saxony-Anhalt, Germany (Manurung et al., 2005)
Eupteryx atropunctata	20	Primarily on mallow (*Malva* spp.), sage (*Salvia officinalis)* and potato (*Solanum tuberosum*)	p	e	2	Le Quesne & Payne, 1981
Euscelis incisus	10	Grassland	o2	e, N	2 §	§ 3rd & 4th instar nymphs of 3rd generation may overwinter in mild winters (Müller, 1981)
Zyginidia scutellaris	10	Grassland	o1	A	3	Waloff, 1994
Psammotettix confinis	8	Grassland	o1	e	2	Waloff & Solomon, 1973
Errastunus ocellaris	5	Grassland	o1	e	2	Waloff & Solomon, 1973; Waloff & Thompson, 1980
Anoscopus albifrons	4	Grassland	o1	e	1	Nickel & Remane, 2002
Eupteryx urticae	3	Nettle (*Urtica dioica*) and spreading pellitory (*Parietaria judaica*)	m1	e	2	Stewart, 1988
Muellerianella brevipennis	2	Tussock grass (*Deschampsia cespitosa)*	m1	e	1–2	Nickel & Remane, 2002
Cicadula quadrinotata	2	Damp grasslands, rushes and sedges	m2?	e	1–2	Nickel & Remane, 2002
Empoasca decipiens	2	Low vegetation, vegetable crops, and fruit trees	p	A	2 + part 3	Alford, 2014
Lindbergina aurovittata	2	Various deciduous trees (esp. oak – *Quercus robur*) and brambles (*Rubus* spp.)	p	e	2	Nickel & Remane, 2002. In Wales, the first generation is found on brambles, the second on other deciduous trees (Claridge & Wilson, 1978)
Alnetoidea alneti	2	Deciduous trees	p	e	1–2	1 generation in South Wales (Claridge & Wilson, 1976); 2 generations in Germany (Nickel & Remane, 2002)

* Habitat type. Taken from various sources including Nickel (2003) and http://www.britishbugs.org.uk/ ‡ Host plant specificity (from Nickel & Remane, 2002): p – polyphagous, o1 –1st degree oligophagous (1 plant family), o2 – 2nd degree oligophagous (2 plant families or less than 5 species of less than 5 families), m1 – 1st degree monophagous (1 plant species), m2 – 2nd degree monophagous, (1 plant genus). e – egg, N – nymph, A – adult.

Species' habitat associations

The species caught are nearly all eurytopic or pioneer species with a wide geographic range, feeding on ruderal plants (such as nettle (*Urtica dioica*) in the case of *Eupteryx urticae*) or vegetable crops (e.g. *Empoasca decipiens*) and exploiting highly disturbed habitats such as intensively-managed grasslands or cereal cultivations (*J. pellucida, D. pulicaris, Z. scutellaris*) (Table 4). Only two species are arboricolous, *Lindbergina aurovittata* and *Alnetoidea alneti*, both of which are polyphagous, an unusual strategy for tree-dwellers. Generally, the species caught were polyphagous or 1st degree oligophagous (according to the categorisation of Nickel & Remane, 2002) (see Table 4).

DISCUSSION

Most of our predictions, based on the results of previous studies in various regions of the world on migration in Auchenorrhyncha, were supported. Unsurprisingly, all individuals in the aerial samples were macropterous. This characteristic, together with the sampling height, indicates that all individuals caught were actively migrating rather than being accidently caught up in convective up-draughts. In fact, small insects aloft in daytime convective conditions display distinctive behaviours with respect to the air column in which they are flying (Wainwright et al., 2017).

Aerial densities

Aerial densities of Auchenorrhyncha estimated from our samples were rather low, although not unusually so, for

small insects flying at these altitudes in Britain (c.f. Johnson, 1969). For comparison, we note that aerial densities of the brown planthopper (*N. lugens*) in south-east Asia can be two orders of magnitude higher during peak migration periods (see Table 10.2 in Drake & Reynolds, 2012).

Diel flight periodicity

Information on diel flight periodicity from our sampling indicates that migration in British Auchenorrhyncha, contrary to our initial hypothesis, is largely a daytime or crepuscular activity. This is in distinct contrast to the long nocturnal migrations found in some North American and East Asian species (e.g. Taylor & Reling, 1986; Riley et al., 1991; Carlson et al., 1992; Kisimoto & Rosenberg, 1994; Reynolds et al., 1999). This may well be because nocturnal air temperatures in Britain and northern Europe are often below thresholds for flight (Raatikainen, 1967; Raatikainen & Vasarainen, 1973), but daytime flight does have the advantage that, during sunny weather, migrants can utilise convective lift to gain height, thus reducing power consumption needed for migratory flight. As mentioned above, many small migratory insect taxa are similarly adapted (Wainwright et al., 2017).

Effects of wind speed and direction

The reason for increased aerial densities associated with high wind speeds is not clear, although we note that in some aphids, much migration takes place in fairly windy weather (lulls in the wind permit take-off) (Johnson, 1954; Walters & Dixon, 1984). The lack of an association with any particular wind direction accords with small insects like aphids that do not seem to fly preferentially on winds from a particular direction (Taylor et al., 1979; Hu et al., 2016), although the leafhopper *E. fabae* in northeastern USA constitutes a known exception. In late summer, *E. fabae* ascending at dusk show an adaptive preference for flight on winds from the north which occur immediately after the passage of a cold front (Taylor & Reling, 1986; Shields & Testa, 1999) – in this case, the increased flight activity seems to be stimulated by falling air pressure.

Voltinism, phenology, overwintering stage and sex-ratio in common migrant species

Auchenorrhyncha assemblages in relatively stable undisturbed habitats such as low-input grasslands tend to be dominated by univoltine species (Novotny, 1994a, 1995; Nickel, 2003; Nickel & Achtziger, 2005). Conversely, species found in disturbed habitats tend to be bivoltine or polyvoltine. The great majority of species in our study belonged to the latter ecological grouping. Some bivoltine leafhopper species show different levels of flight activity between generations (Nickel, 2003) but even so, having more than one generation per year would enhance the ability of the species to track temporally variable stands of host-plants.

J. pellucida is bivoltine in England with flight in both generations, but with macroptery particularly dominant in adults of the second generation (Waloff, 1973). The specimens caught in in our study in July evidently represent second generation migrants (c.f. Fig. 4 in Waloff, 1973). The two peaks of *A. pascuellus,* in early and late summer, probably represent the migration of the first and second generations of this bivoltine species (see seasonal occurrence of adults in Waloff & Solomon, 1973). Among the species of grassland leafhoppers she studied, Waloff (1973) inferred that *A. pascuellus* had rather low powers of dispersal, based on the relationship between numbers in traps at 1.2 and 9 m above ground. While not directly refuted by our data – we had no information on ground populations – this contention seems unlikely in view of our high-altitude catches. Specimens of the multivoltine *Z. scutellaris*, captured between mid-June and mid-July, were likely to have been first generation adults (Waloff, 1994). The large numbers of *Z. scutellaris* caught in French suction traps at the end of July / beginning of August was attributed to a generation produced on maize cultivations (della Giustina & Balasse, 1999). The two *Macrosteles* females (of unknown species) caught in our samples in June were presumably first generation individuals. *Macrosteles sexnotatus* was the most abundant species in Freeman's (1939) study, in which captures in June and September represent the first and second generation adults, respectively, according to Waloff & Solomon's (1973) phenology for *M. laevis*/*sexnotatus* in southern England.

The leafhoppers caught by our aerial trapping were mostly species which overwinter in the egg stage, although the planthopper *J. pellucida* overwinters as a nymph. This seems to be the typical situation in the cicadomorph and fulgoromorph Auchenorrhyncha respectively (see Table 37 in Nickel, 2003), however, so it is not clear whether this difference represents an ecological adaption or just a phylogenetic constraint. *Zyginidia scutellaris* and *E. decipiens* are exceptions to the usual leafhopper pattern in that they overwinter as adults, but these species are unusual in any case as they tend to multivoltinism in England. It should be noted that our sampling period did not include very early (March) or late (November) in the season, with the consequence that we may have missed other species that often overwinter as adults (e.g. *Balclutha* spp., *Zygina* spp. and some Idiocerinae). However, Freeman (1939) who did sample from March to November in one year (1935) from his masts in Lincolnshire, caught very few Auchenorrhyncha outside the May−September period (*N. lineatus* was trapped in November).

Our prediction that migrating individuals would have an equal sex ratio was supported by *J. pellucida* but not *A. pascuellus*. The female-biased sex ratio in *A. pascuellus* in our samples differs from the near-equal sex ratio (1.1♀ : 1♂) in Waloff's (1973) suction trap samples taken nearer the ground (at or below 12.2 m).

Species composition of aerial samples

The qualitative similarity between our catches of Auchenorrhyncha and those in suction traps at 12.2 m above ground in France based on much wider geographical and seasonal coverage (della Giustina & Balasse, 1999), gives us confidence that we are sampling similar ecological phenomena.

The dominance of *J. pellucida* in our catches is, perhaps, not surprising as the species is very common; Nickel (2003) states that it is probably the most common auchenorrhynchan in most parts of cultivated lowlands in Central Europe. It is also a noted migrant, often contributing a high proportion of the catch in traps at heights of ~10–12 m above ground in southern England (Waloff, 1973), France (della Giustina & Balasse, 1999) and Finland (Raatikainen & Vasarainen, 1973), although not locally the most abundant planthopper. It is wing-polymorphic, but it is one of rather few delphacids in which macropters dominate, presumably reflecting its dispersal tendencies. It is a vector of several plant disease agents including Oat sterile dwarf virus and European wheat striate mosaic virus (Brčák, 1979; Lindsten, 1979).

The occurrence of certain individual species in our catches deserves comment. The large and distinctive leafhopper, *Athysanus argentarius*, appeared once in our aerial samples and has been discussed previously (Salmon & Chapman, 2000) in respect of its northward range expansion in recent years in Britain. Teraguchi (1986) referred to *A. argentarius* as a classic example of the oogenesis/flight syndrome of Johnson (1969), as most of the catch in his aerial traps were females, but only a very small percentage of these were sexually mature.

The presence of the leafhopper *Anoscopus albifrons*, albeit in small numbers (4), is remarkable given that this species is normally considered to dwell close to the ground, being most frequently sampled by pitfall traps or powerful suction sampling (Stewart, 2002). The same comment would apply to *Anaceratagallia ribauti*, although only a singleton of this species was caught.

Finally, we note that catches of small insects over the sea far from land are also indicative of windborne migration; in this context two '*Empoasca flavescens*' [now *Empoasca vitis* (Göthe)] and one *J. pellucida* were reported in samples taken in 1938 over the North Sea (with nets attached to ships' mast-heads) (Hardy & Cheng, 1986).

CONCLUSIONS

The species caught by aerial trapping were certainly not a random assortment of the approximately 150 Auchenorrhyncha regarded as common in Britain (see http://www.ledra.co.uk/species.html) but, in the main, they seem to be a guild of species exploiting the same class of resources in a similar manner, with migration constituting an important element of their life-cycle. In the first instance, migration abilities will of course depend on macroptery, and will also be related to age and sexual maturity. Where the matter has been considered, migratory flight in European Auchenorrhyncha seems to occur fairly soon (a few days) after the appearance of the first adults, e.g. in *J. pellucida* and *D. pulicaris* (Raatikainen, 1967, Raatikainen & Vasarainen, 1973), and this timing would also have to take into account any periods where weather was unfavourable for flight. So we can conclude that migration occurs in sexually *immature* adults, and that mature ones tend to 'flit' or even show loss of flight capacity (Waloff, 1973). Thus, several of the Auchenorrhyncha considered here show evidence of the oogenesis-flight syndrome (as found in planthoppers and leafhoppers from other regions, e.g. Teraguschi, 1986; Kisimoto & Rosenberg, 1994; Shields & Testa, 1999).

After these physiological and morphological aspects of the migration syndrome (Dingle, 2014; Chapman et al., 2015) are taken into account, the species found in our samples exemplify a colonising 'life-style' with the associated relationships between migration propensity and the durational stability and isolation of the habitat. In fact, several careful assessments have confirmed the relationship between the migratory capability of Auchenorrhyncha and the ephemerality of their habitats (e.g. Denno et al., 1991, 1996, 2001; Novotný, 1994b), with the proviso that species associated with three-dimensional habitats (trees, tall herbs) tend to exhibit monomorphic macroptery because of the need for wings to negotiate around the complex host-plant architecture (Waloff, 1983; Denno et al., 2001). The species regularly encountered in aerial samples (Table 4) tend to be common 'r-selected' opportunists, characteristically found in disturbed grasslands or in other early-successional and ephemeral habitats (Morris, 1990a; Nickel, 2003; Nickel & Hildebrandt, 2003). They are also characterized by low food specificity – polyphagous species are known to be associated with transient habitats, unlike monophagous specialists, which prefer more stable ones (Novotny, 1994a; Nickel, 2003). Arboricolous species were much less frequently captured in this, and previous, studies of aerial migration, and those that were caught tended to be polyphagous on a range of deciduous trees.

In summary, we consider that the captures of Auchenorrhyncha documented here do not represent haphazard events, but are indicative of regular migrations in the upper air as an adaptation to a colonising way of life. Clearly more data are required to support this view, particularly in the case of the species where only singletons were collected, but we hope that this preliminary contribution will stimulate further work on the migration syndromes of this group of insects.

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REFERENCES

Alford D.V. 2014: *Pests of Fruit Crops: A Color Handbook. 2nd ed.* CRC Press, Boca Raton, FL, 462 pp.

Berland L. 1935: Premier résultats de mes recherches en avion sur la faune et la flore atmosphériques. — *Ann. Soc. Entomol. Fr.* **104**: 73–96.

Brčák J. 1979: Leafhopper and planthopper vectors of plant disease agents in central and southern Europe. In Maramorosch K. & Harris K.F. (eds): *Leafhoppers Vectors and Plant Disease Agents*. Academic Press, New York, pp. 97–154.

Carlson J.D., Whalon M.E., Landis D.A. & Gage S.H. 1992: Springtime weather patterns coincident with long-distance migration of potato leafhopper into Michigan. — *Agric. For. Meteorol.* **59**: 183–206.

Chapman J.W., Reynolds D.R., Smith A.D., Smith E.T. & Woiwod I.P. 2004: An aerial netting study of insects migrating at high-altitude over England. — *Bull. Entomol. Res.* **94**: 123–136.

Chapman J.W., Reynolds D.R. & Wilson K. 2015: Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. — *Ecol. Lett.* **18**: 287–302.

Chasen E.M., Dietrich C., Backus E.A. & Cullen E.M. 2014: Potato leafhopper (Hemiptera: Cicadellidae) ecology and integrated pest management focused on alfalfa. — *J. Integr. Pest Manag.* **5**: A1–A8.

Claridge M.F. & Wilson M.R. 1976: Diversity and distribution patterns of some mesophyll-feeding leafhoppers of temperate woodland canopy. — *Ecol. Entomol.* **1**: 231–250.

Claridge M.F. & Wilson M.R. 1978: Seasonal changes and alternation of food plant preference in some mesophyll-feeding leafhoppers. — *Oecologia* **37**: 247–255.

della Giustina W. & Balasse H. 1999: Gone with the wind: Homoptera Auchenorrhyncha collected by the French network of suction traps in 1994. — *Marburg. Entomol. Publ.* **3**: 7–42.

Denno R.F., Roderick G.K., Olmstead K.L. & Dobel H.G. 1991: Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. — *Am. Nat.* **138**: 1513–1541.

Denno R.F., Roderick G.K., Peterson M.A., Huberty A.F., Döbel H.G., Eubanks M.D., Losey J.E. & Langellotto G.A. 1996: Habitat persistence underlies the intraspecific dispersal strategies of planthoppers. — *Ecol. Monogr.* **66**: 389–408.

Denno R.F., Gratton C. &. Langellotto G.A. 2001: Significance of habitat persistence and dimensionality in the evolution of insect dispersal strategies. In Woiwod I.P., Reynolds D.R. & Thomas C.D. (eds): *Insect Movement: Mechanisms and Consequences*. CAB International, Wallingford, pp. 235–259.

Dingle H. 2014: *Migration: The Biology of Life on the Move. 2nd ed.* Oxford University Press, Oxford, x + 326 pp.

Drake V.A. & Reynolds D.R. 2012: *Radar Entomology: Observing Insect Flight and Migration*. CABI, Wallingford, xviii + 489 pp.

Freeman J.A. 1939: *Studies in the Distribution of Insects by Aerial Currents. A Contribution to the Study of Windborne Insects with Special Reference to Vertical Distribution and Dispersal*. PhD Thesis, University College, Hull, UK.

Freeman J.A. 1945: Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet. — *J. Anim. Ecol.* **14**: 128–154.

Ghauri M.S.K. 1983: A case of long-distance dispersal of a leafhopper. In Knight W.J., Pant N.C., Robertson T.S. & Wilson M.R. (eds): *1st International Workshop on Leafhoppers and Planthoppers of Economic Importance*. Commonwealth Institute of Entomology, London, pp. 249–255.

Glick P.A. 1939: *The Distribution of Insects, Spiders and Mites in the Air*. *Technical Bulletin No. 673*, United States Department of Agriculture, Washington, D.C., 151 pp.

Glick P.A. 1960: *Collecting Insects by Airplane, with Special Reference to Dispersal of the Potato Leafhopper. Technical Bulletin No. 1222*, United States Department of Agriculture, Washington D.C., 28 pp.

Günthart H. 1988: Comparison of the vertical distribution of leafhoppers – trapped between 5 and 155 m above the ground – with the ground population. In Vidano C. & Arzone A. (eds): *6th Auchenorrhyncha Meeting, Turin, Italy, September 7–11, 1987*. Consiglio Nazionale delle Ricerche, Spezial Project IPRA, Italy, pp. 379–386.

Hardy A.C. & Cheng L. 1986: Studies in the distribution of insects by aerial currents. III. Insect drift over the sea. — *Ecol. Entomol.* **11**: 283–290.

Hardy A.C. & Milne P.S. 1938: Studies in the distribution of insects by aerial currents. Experiments in aerial tow-netting from kites. — *J. Anim. Ecol.* **7**: 199–229.

Heong K.L. & Hardy B. 2009: *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia*. International Rice Research Institute, Los Baños, Philippines, 460 pp.

Hothorn T., Bretz F. & Westfall P. 2008: Simultaneous inference in general parametric models. — *Biometrical J.* **50**: 346–363.

Hu G., Lim K.S., Horvitz N., Clark S.J., Reynolds D.R., Sapir N. & Chapman J.W. 2016: Mass seasonal bioflows of high-flying insect migrants. — *Science* **354**: 1584–1587.

Johnson C.G. 1954: Aphid migration in relation to weather. — *Biol. Rev.* **29**: 87–118.

Johnson C.G. 1969: *Migration and Dispersal of Insects by Flight*. Methuen, London, xxii + 763 pp.

Kisimoto R. & Rosenberg L.J. 1994: Long-distance migration in delphacid planthoppers. In Denno R.F. & Perfect T.J. (eds): *Planthoppers: Their Ecology and Management*. Chapman and Hall, New York, pp. 302–322.

Le Quesne W.J. 1960: *Hemiptera: Fulgoromorpha. Handbooks for the Identification of British Insects. Vol II, Part 3*. Royal Entomological Society, London, 68 pp.

Le Quesne W.J. 1965: *Hemiptera Cicadomorpha (excluding Deltocephalinae and Typhlocybinae). Handbooks for the Identification of British Insects. Vol II, Part 2(a)*. Royal Entomological Society, London, 64 pp.

Le Quesne W.J. 1969: *Hemiptera Cicadomorpha Deltocephalinae. Handbooks for the Identification of British Insects. Vol II, Part 2(b)*. Royal Entomological Society, London, 84 pp.

Le Quesne W.J. & Payne K.R. 1981: *Cicadellidae (Typhlocybinae) with a Checklist of the British Auchenorrhyncha (Hemiptera, Homoptera). Handbooks for the Identification of British Insects. Vol II, Part 2(c)*. Royal Entomological Society, London, 95 pp.

Lewis T. & Taylor L.R. 1964: Diurnal periodicity of flight by insects. — *Trans. R. Entomol. Soc. Lond.* **116**: 393–479.

Lindsten K. 1979: Planthopper vectors and plant disease agents in Fennoscandia. In Maramorosch K. & Harris K.F. (eds): *Leafhoppers Vectors and Plant Disease Agents*. Academic Press, New York, pp. 155–178.

Macaulay E.D.M., Tatchell G.M. & Taylor L.R. 1988: The Rothamsted Insect Survey '12-metre' suction trap. — *Bull. Entomol. Res.* **78**: 121–129.

Magurran A.E. 2003: *Measuring Biological Diversity*. Wiley-Blackwell, Oxford, 264 pp.

Manurang B., Witsack W., Mehner S., Gruntzig M. & Fuchs E. 2005: Studies on biology and population dynamics of the leafhopper *Psammotettix alienus* Dahlb. (Homoptera: Auchenorrhyncha) as vector of Wheat dwarf virus (WDV) in Saxony-Anhalt, Germany. — *Z. Pflanzenkr. Pflanzensch.* **112**: 497–507.

Morris M.G. 1990a: The Hemiptera of two sown calcareous grasslands. I. Colonization and early succession. — *J. Appl. Ecol.* **27**: 367–378.

Morris M.G. 1990b: The Hemiptera of two sown calcareous grasslands. II. Differences between treatments. — *J. Appl. Ecol.* **27**: 379–393.

Muller H.J. 1981: Die Bedeutung der Dormanzformen fur die Populationsdynamik der Zwergzikade *Euscelis incisus* (Kbm.) (Homopt., Cicadellidae). — *Zool. Jb. Syst.* **106**: 314–334.

Nickel H. 2003: *The Leafhoppers and Planthoppers of Germany (Hemiptera, Auchenorrhyncha)*: *Patterns and Strategies in a Highly Diverse Group of Phytophagous Insects*. Pensoft, Sofia & Moscow and Goecke & Evers, Keltern, 460 pp.

Nickel H. & Achtziger R. 2005: Do they ever come back? Responses of leafhopper communities to extensification of land use. — *J. Insect Conserv.* **9**: 319–333.

Nickel H. & Hildebrandt J. 2003: Auchenorrhyncha communities as indicators of disturbance (Insecta, Hemiptera) – a case study from the Elbe flood plains (northern Germany). — *Agric. Ecosyst. Environ.* **98**: 183–199.

Nickel H. & Remane R. 2002: Artenliste der Zikaden Deutschlands, mit Angabe von Nährpflanzen, Nahrungsbreite, Lebenszyklus, Areal und Gefährdung (Hemiptera, Fulgoromorpha et Cicadomorpha). — *Beitr. Zikadenk.* **5**: 27–64.

Novotný V. 1994a: Association of polyphagy in leafhoppers (Auchenorrhyncha, Hemiptera) with unpredictable environments. — *Oikos* **70**: 223–232.

Novotný V. 1994b: Relation between temporal persistence of host plants and wing length in leafhoppers (Auchenorrhyncha, Hemiptera). — *Ecol. Entomol.* **19**: 168–176.

Novotný V. 1995: Relationships between life histories of leafhoppers (Auchenorrhyncha – Hemiptera: and their host plants (Juncaceae, Cyperaceae, Poaceae). — *Oikos* **73**: 33–42.

Otuka A. 2013: Migration of rice planthoppers and their vectored re-emerging and novel rice viruses in East Asia. — *Front. Microbiol.* **4**: 309, 11 pp.

Otuka A., Matsumura M., Sanada-Morimura S., Takeuchi H., Watanabe T., Ohtsu R. & Inoue H. 2010: The 2008 overseas mass migration of the small brown planthopper, *Laodelphax striatellus*, and subsequent outbreak of rice stripe disease in western Japan. — *Appl. Entomol. Zool.* **45**: 259–266.

R Core Team 2016: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, URL: https://www.R-project.org/.

Raatikainen M. 1967: Bionomics, enemies and population dynamics of *Javesella pellucida* (F.) (Hom., Delphacidae). — *Ann. Agric. Fenn. (Suppl. 2)* **6**: 1–149.

Raatikainen M. & Vasarainen A. 1973: Early- and high-summer flight periods of leafhoppers. — *Ann. Agric. Fenn.* **12**: 77–94.

Reynolds D.R., Mukhopadhyay S., Riley J.R., Das B.K., Nath P.S. & Mandal S.K. 1999: Seasonal variation in the windborne movement of insect pests over northeast India. — *Int. J. Pest Manag.* **45**: 195–205.

Reynolds D.R., Nau B.S. & Chapman J.W. 2013: High-altitude migration of Heteroptera in Britain. — *Eur. J. Entomol.* **110**: 483–492.

Reynolds D.R., Reynolds A.M. & Chapman J.W. 2014: Non-volant modes of migration in terrestrial arthropods. — *Anim. Migrat.* **2**: 8–28.

Riley J.R., Cheng X.-N., Zhang X.-X., Reynolds D.R., Xu G.-M., Smith A.D., Cheng J.-Y., Bao A.-D. & Zhai B.-P. 1991: The long-distance migration of *Nilaparvata lugens* (Stal) (Delphacidae) in China: Radar observations of mass return flight in the autumn. — *Ecol. Entomol.* **16**: 471–489.

Rose D.J.W. 1978: Epidemiology of maize streak disease. — *Annu. Rev. Entomol.* **23**: 259–282.

Salmon M.A. & Chapman J.W. 2000: On the history and distribution of *Athysanus argentarius* Metcalf (Hem.: Cicadellidae) in Britain. — *Br. J. Entomol. Nat. Hist.* **13**: 91–93.

Shields E.J. & Testa A.M. 1999: Fall migratory flight initiation of the potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae): observations in the lower atmosphere using remote piloted vehicles. — *Agric. For. Meteorol.* **97**: 317–330.

Southwood T.R.E. 1960: The flight activity of Heteroptera. — *Trans. R. Entomol. Soc. Lond.* **112**: 173–220.

Southwood T.R.E. 1962: Migration of terrestrial arthropods in relation to habitat. — *Biol. Rev.* **37**: 171–214.

Stewart A.J.A. 1988: Patterns of host plant utilisation by leafhoppers in the genus *Eupteryx* (Hemiptera: Cicadellidae) in Britain. — *J. Nat. Hist.* **22**: 357–379.

Stewart A.J.A. 2002: Techniques for sampling Auchenorrhyncha in grasslands. — *Denisia* **4**: 491–512.

Taylor L.R. 1974: Insect migration, flight periodicity and the boundary layer. — *J. Anim. Ecol.* **43**: 225–238.

Taylor R.A.J. 1985: Migratory behavior in the Auchenorryncha. In Nault L.R. & Rodriguez J.G. (eds): *The Leafhoppers and Planthoppers*. Wiley, New York, pp. 259–287.

Taylor R.A.J. 1989: Potato leafhopper migration: the mystery of the return migration. — *Misc. Publ. Entomol. Soc. Am.* **72**: 42–52.

Taylor R.A.J. & Reling D. 1986: Preferred wind direction of long-distance leafhopper (*Empoasca fabae*) migrants and its relevance to the return migration of small insects. — *J. Anim. Ecol.* **55**: 1103–1114.

Taylor L.R., Woiwod I.P. & Taylor R.A.J. 1979: The migratory ambit of the hop aphid and its significance in aphid population dynamics. — *J. Anim. Ecol.* **48**: 955–972.

Taylor P.S., Shields E.J., Tauber M.J. & Tauber C.A. 1995: Induction of reproductive diapause in *Empoasca fabae* (Homoptera, Cicadellidae) and its implications regarding southward migration. — *Environ. Entomol.* **24**: 1086–1095.

Teraguchi S.E. 1986: Migration patterns of leafhopper (Homoptera: Cicadellidae) in an Ohio old field. — *Environ. Entomol.* **15**: 1199–1211.

Wainwright C.E., Stepanian P.M., Reynolds D.R. & Reynolds A.M. 2017: The movement of small insects in the convective boundary layer: linking patterns to processes. — *Sci. Rep.* **7**: 5438, 8 pp.

Waloff N. 1973: Dispersal by flight of leafhoppers (Auchenorrhyncha: Homoptera). — *J. Appl. Ecol.* **10**: 705–730.

Waloff N. 1983: Absence of wing polymorphism in the arboreal, phytophagous species of some taxa of temperate Hemiptera: an hypothesis. — *Ecol. Entomol.* **8**: 229–232.

Waloff N. 1994: Observations on *Zyginidia scutellaris* (Herrich-Schaeffer), Auchenorrhyncha: Typhlocybinae, Cicadellidae. — *The Entomologist* **113**: 20–27.

Waloff N. & Solomon M.G. 1973: Leafhoppers (Auchenorrhyncha: Homoptera) of acidic grassland. — *J. Appl. Ecol.* **10**: 189–212.

Waloff N. & Thompson P. 1980: Census data of populations of some leafhoppers (Auchenorrhyncha, Homoptera) of acid grassland. — *J. Anim. Ecol.* **49**: 395–416.

Walters K.F.A. & Dixon A.F.G. 1984: The effect of temperature and wind on the flight activity of cereal aphids. — *Ann. Appl. Biol.* **104**: 17–26.

Wilson M., Stewart A., Biedermann R., Nickel H. & Niedringhaus R. 2015: *The Planthoppers and Leafhoppers of Britain and Ireland*. Wissenschaftlich Akademischer Buchvertrieb-Fründ, Scheeßel, 138 pp.

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